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The African Penguin *Spheniscus demersus* should be considered Critically Endangered

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The African Penguin *Spheniscus demersus* has been considered a threatened species since 1984 and, aside from a short period around 2000, its population has been in constant decline since at least the 1950s. By combining counts of the numbers of breeding pairs made at 26 colonies in South Africa and Namibia between 1979 and 2023 with Bayesian state–space models we reassess the species' conservation status. The breeding population has declined by 77.8% (95% credible intervals: 71.8–84.6%) over the last 30 years (3 generations), from ~44 300 breeding pairs in 1993 to ~9 900 pairs in 2023. This falls just below the threshold for a global IUCN Red List status of Critically Endangered (CR) under criterion A2. However, the decline in Namibia exceeds that threshold at the national level (30-year decline = 82.4%, 78.2–86.2%) following the loss of ~3 600 breeding pairs there in the last 5 years. In South Africa, the Western Cape population is now declining at <1.5% per annum, but the annual rate of decline in the Eastern Cape has worsened substantially, reaching 13% over the last 10 years. Overall, the global population has more than halved in the last decade and has fallen below 10 000 pairs for the first time. Moreover, “moving window reductions” over 3 generations using observed and projected population trajectories (up to the year 2033) indicate that the decline of the African Penguin population will exceed the 80% CR threshold (under criterion A4ab) with a high probability by 2028. Accordingly, we propose that the African Penguin should be transferred to the IUCN Red List category Critically Endangered.

Le Manchot du Cap devrait être classifié comme En Danger Critique

Le Manchot du Cap *Spheniscus demersus* est considéré comme une espèce menacée depuis 1984 et, à l'exception d'une courte période autour de 2000, sa population est en déclin constant depuis au moins les années 1950. En combinant les comptages du nombre de couples reproducteurs effectués dans 26 colonies d'Afrique du Sud et de Namibie entre 1979 et 2023 avec des modèles espace-état bayésiens, nous réévaluons l'état de conservation de l'espèce. La population reproductrice a diminué de 77.8% (intervalles crédibles à 95%: 71.8–84.6%) au cours des 30 dernières années (3 générations), passant de ~44 300 couples reproducteurs en 1993 à ~9 900 couples en 2023. Ce chiffre se situe juste en dessous du seuil de 80% qui justifie sa classification dans la liste rouge de l'IUCN comme «en danger critique d'extinction» (CR) selon le critère A2. Cependant, le déclin en Namibie dépasse ce seuil au niveau national (déclin sur 30 ans = 82.4: 78.2–86.2%) suite à la perte de ~3 600 couples reproducteurs au cours des 5 dernières années. En Afrique du Sud, la population du Western Cape décline maintenant à un rythme inférieur à 1.5 % par an, mais le taux annuel de déclin dans le Eastern Cape s'est considérablement aggravé, atteignant 13% au cours des 10 dernières années. Globalement, la population mondiale a diminué de plus de moitié au cours de la dernière décennie et est passée pour la première fois sous la barre des 10 000 couples. De plus, les réductions de la 'fenêtre mobile' sur 3 générations utilisant les trajectoires de population observées et projetées (jusqu'en 2033) indiquent que le déclin de la population de Manchots du Cap dépassera le seuil de 80% de CR (selon le critère A4ab) avec une forte probabilité d'ici 2028. En conséquence, nous suggérons que le Manchot du Cap soit désormais considéré comme étant En Danger Critique.

Keywords: conservation status, extinction risk, IUCN Red List, JARA, Just Another Red-list Assessment, population size reduction, southern Africa

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Introduction

The African Penguin *Spheniscus demersus* is one of seven seabird species endemic to the Benguela upwelling ecosystem of southwestern Africa, where it currently breeds at 26 localities clustered in three regions: South Africa's Western Cape and Eastern Cape provinces and central/southern Namibia. Though the total population size at the start of the 20th century is unknown, the African Penguin may have been the region's most abundant seabird with possibly ~1.5–3 million individuals across its range (Shannon and Crawford 1999; Crawford et al. 2007). By 1956 only ~0.3 million individuals remained, and the population has declined consistently since then, apart from a brief recovery in the late 1990s and early 2000s (Crawford et al. 2011; Sherley et al. 2020a; Figure 1). Since the first formal attempts to estimate the species' population size in 1956 (Rand 1963a,b), its conservation status has been reviewed several times (e.g. Frost et al. 1976; Brooke 1984; Shelton et al. 1984; Kemper et al. 2007a; Sherley et al. 2020a). The African Penguin was first considered to have met the criteria to be listed as Vulnerable (VU) in 1984 (Brooke 1984; Shelton et al. 1984) and as Endangered (EN) in 2007 (Kemper et al. 2007a), with formal IUCN Red List assessments following suite in 2000 (VU), 2010 (EN) and 2016 (EN). Here, we use updated counts of the numbers of breeding pairs made at 26 colonies in South Africa and Namibia between 1979 and 2023 (representing >99% of the known population), combined with the Bayesian state-space models implemented via the JARA R package (<https://github.com/Henning-Winker/JARA>) to consider the current population size and reassess the conservation status of the African Penguin under criterion A2ab and A4ab (see Table 1). We follow the methods outlined in Sherley et al. (2020a), which reassessed the species' conservation status up to 2019. We do not discuss the threats to the African Penguin or drivers underpinning their decline, as these have been discussed extensively elsewhere (e.g. Crawford et al. 2011; Sherley et al. 2020a; Crawford et al. 2022). The state-space models in R were run using three chains of 25 000 iterations each, with a burn-in of 10 000 and a thinning rate of 5. We used a generation length of 10 years (Sherley et al. 2020a; although we explored sensitivity to generation length, with the results summarised in Supplementary Table S1), the "census" model type in JARA, and set the proj.r setting to "GL1" to generate future projections based on the median rate of change over the final 10 years (1 generation length) of the observed data. Full methods detailing how the nest counts are undertaken can be found in Shelton et al. (1984) and Crawford et al. (2011), and are summarised in Sherley et al. (2020a). Full details of the JARA state-space framework can be found in Sherley et al. (2020a,b) and Winker et al. (2020), and the full dataset and code needed to reproduce the analysis reported here, along with all of the JARA outputs, are available on GitHub (https://github.com/rbsherley/AP_IUCN_CR).

Global population and Red List status under criterion A2

The African Penguin population has declined from ~44 300 breeding pairs in 1993 to ~9 900 pairs in 2023.

This corresponds to an estimated decline of 77.8% (95% credible intervals: 71.8–84.6%) over the last 3 generations (3G), with 77% of the posterior distribution falling within the range for Endangered (EN) status under criterion A2ab (past decline), and 23% meeting the criteria for Critically Endangered (CR; Figure 1A). This represents a worsening situation relative to an assessment conducted up to 2019, where the decline over 3G was 64.1% (51.0–77.5%; Sherley et al. 2020a). Although the observed decline falls just short of the 80% threshold for the status of CR, this long-term trend should be viewed in the context of four key observations. First, the global rate of decline over the last 10 years (or 1 generation, 1G) has nearly doubled, from 4.3% per annum in the 2019 assessment (Sherley et al. 2020a) to 7.9% (3.9–11.8%) as reported here. Second, the annual rate of decline over the last 10 years (1G) was 9.9% (3.1–17.4%) in Namibia and 12.9% (5.9–20.6%) in the Eastern Cape, South Africa. Third, this is the first time that the global breeding population of African Penguins has fallen below 10 000 pairs. To contextualise this, three islands each held more breeding pairs than the current global population for periods between 1979 and 2007: Dassen Island had ~11 000 pairs as recently as 2007; Dyer Island had >10 000 pairs until 1990; and St Croix Island held >12 000 pairs until 2003. There are also now considerably fewer individual African Penguins in the population (~31 700) than the number affected by the MV Treasure oil spill in 2000, when ~38 500 individuals were either oiled, cleaned and released, or relocated to stop them becoming oiled (Crawford et al. 2000). And fourth, the global population has more than halved in the last decade, largely because of the combined loss of >12 500 breeding pairs in Namibia (~4 450) and the Eastern Cape (~8 100) since 2015. In other words, substantially (>25%) more birds have been lost in less than 10 years than now remain in the African Penguin population. Thus, it is not unreasonable to be concerned that — if these rates of decline persist — the species could become extinct in the wild by 2035.

Namibia – national Red List status and trend

The African Penguin has been considered Endangered at a national level since 2007 (Kemper et al. 2007a; Kemper 2015), but breeding numbers had been relatively stable at ~5 000 breeding pairs for about two decades between 1997 and 2017. The assessment using data up to 2019 suggested a rate of decline over 3G of 38.1% (23.4%–51.0%) and a national Red List status of Vulnerable (VU) for Namibia (Sherley et al. 2020a). However, the population has subsequently declined sharply, from ~4 800 pairs in 2018 to ~1 200 pairs in 2023 (Figure 1B). Consequently, we recommend that the Namibian population be up-listed to a national Red List status of CR as it exceeds criterion A2ab with 87% probability and median decline over 3G of 82.4% (78.2–86.2%; Figure 1B). Worryingly, the 2023 census detected no breeding pairs at Mercury Island — the colony that had held ~50% of the Namibian population in the period of stability between 1997 and 2017. The 2023 counts also suggest that only one of the Namibian colonies (Halifax

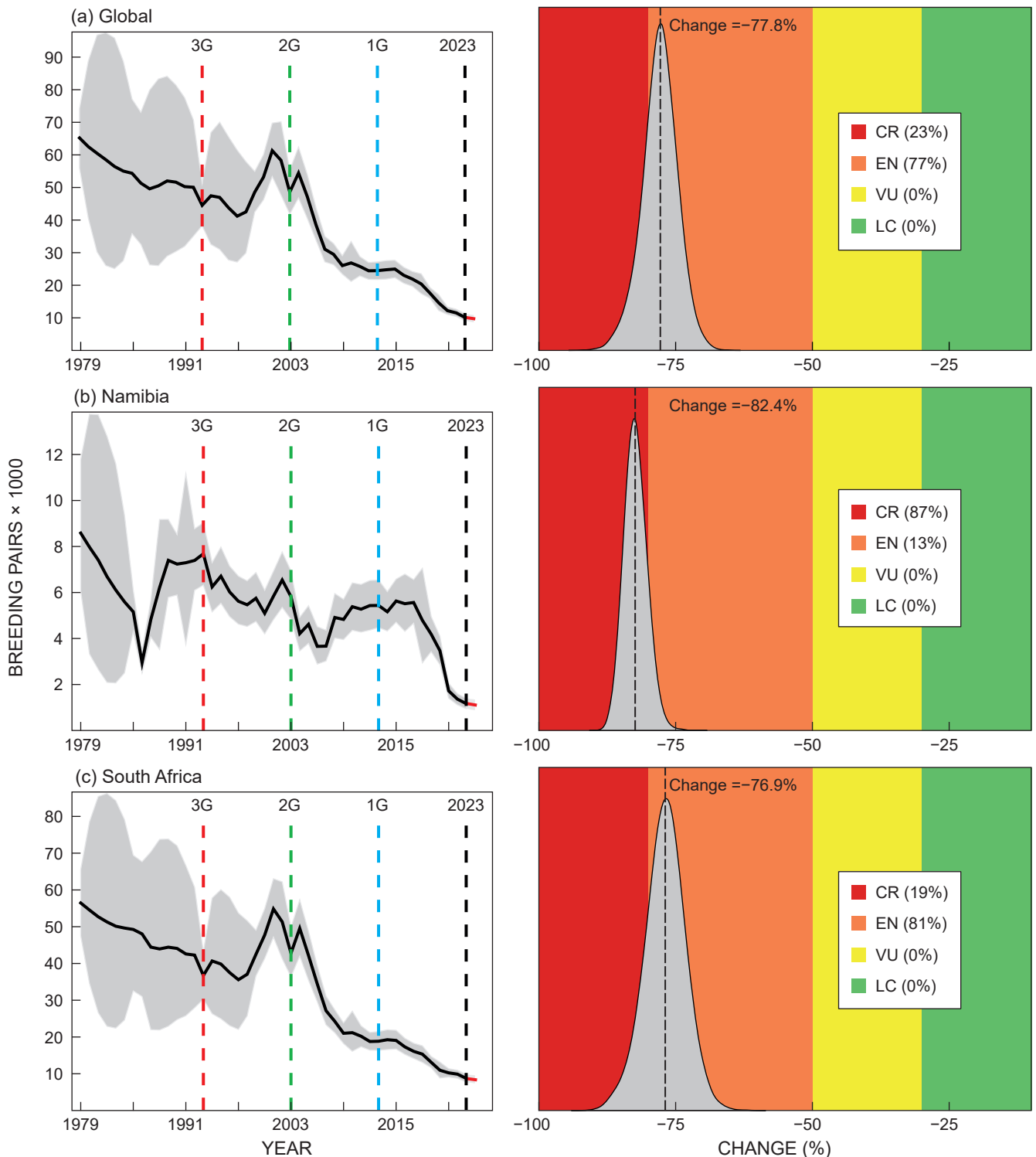


Figure 1: Left panels: The modelled trajectory (black line denotes the posterior median) and 95% highest-posterior-density intervals (HPDI; grey polygon) for the African Penguin *Spheniscus demersus* based on nest counts made between 1979 and 2023: (a) the global population at 26 breeding colonies; (b) the Namibian population at 7 colonies; and (c) the South African breeding population at 19 colonies. The 10-year generation lengths before 2023 are denoted by a blue dashed line (1G, 2013), a green dashed line (2G, 2003), and a red dashed line (3G, 1993). Right panels: The associated median change (%), dashed line) in the breeding population of African Penguins over three generations (3G) or 30 years (globally, in Namibia only, and in South Africa only) and the corresponding posterior probability (grey polygon) for that change, overlaid on the IUCN thresholds for Red List criterion A2ab (green = Least Concern; yellow = Vulnerable; orange = Endangered; red = Critically Endangered)

Table 1: Summary of IUCN Red List criterion A used to evaluate whether a species belongs in a threatened category, along with the Critically Endangered (CR) and Endangered (EN) thresholds for each of the subcriteria (IUCN 2012). The subcriteria of criterion A assess population size reduction, measured over the longer of 10 years or 3 generations, based on *inter alia* (a) direct observation [cannot be used for criterion A3], and (b) an index of abundance appropriate to the taxon (see IUCN 2012, page 16, for data types c, d and e, which were not used here). Subcriteria A2ab and A4ab were used in this analysis

Subcriteria	Description	CR threshold	EN threshold	Applicable to the African Penguin
A1	Population reduction observed, estimated, inferred, or suspected in the past, where the causes of the reduction are clearly reversible AND understood AND have ceased	≥90%	≥70%	No
A2	Population reduction observed, estimated, inferred, or suspected in the past, where the causes of reduction may not have ceased OR may not be understood OR may not be reversible	≥80%	≥50%	Yes
A3	Population reduction projected, inferred or suspected to be met in the future (up to a maximum of 100 years)			
A4	An observed, estimated, inferred, projected or suspected population reduction where the time period must include both the past and the future (up to a maximum of 100 years in future), and where the causes of reduction may not have ceased OR may not be understood OR may not be reversible			

Island) currently holds more than 500 breeding pairs (see Supplementary Figure S1); dropping below this number empirically implies a <50% probability of still being extant in the next 40 years (Crawford et al. 2001). Moreover, our projections over the next 10 years suggest that four of the seven major colonies in Namibia will be effectively extinct (fewer than 10 pairs) by 2034.

South Africa – national Red List status and regional trends

In South Africa, the breeding population has declined by 76.9% (69.4–84.0%) over the last 3G, to ~8 750 pairs in 2023 (Figure 1C). As in Namibia, this rate of decline has worsened relative to the 2019 assessment where the median decline was 67.7% (52.9–82.5%) over 3G (Sherley et al. 2020a). EN remains the best supported national status in South Africa under criterion A2ab, with 81% of the posterior distribution within the EN decline range (Figure 1C). This national pattern, however, is made up of quite different regional trajectories.

In the Western Cape Province, the population at the seven colonies north of Cape Town (the West Coast region) declined by 75.3% (68.2–81.6%) over the last 3G (versus 68.7% in the 2019 assessment), but a period of rapid decline between 2004 and 2014 was followed by 10 years of relative stability when the population only declined by 0.6% (–5.1% to 6.1%) per annum from ~3 500 pairs in 2014 to ~3 170 pairs in 2023. Meanwhile, the population in the South-West Coast region (the five Western Cape colonies south and east of Cape Town) declined slowly and fairly consistently (at 1.4%: –2.4% to 5.2% per annum), leading to an overall decline of 31.1% (9.6–49.9%) over the last

3G (versus 53.1% in the 2019 assessment), from ~4 300 pairs around 1994 to ~3 100 pairs by 2023. Until recently this trajectory was dominated by the long-term decline at Dyer Island being partially offset by increases at Stony Point and the colony at Simonstown. Over recent years, however, these two mainland colonies have also declined: Stony Point from ~2 460 pairs in 2015 to ~1 260 in 2023, and Simonstown from ~1 100 pairs in 2020 to ~870 in 2023 (see Supplementary Figure S2).

Most concerning is the regional trend in the Eastern Cape. There, the numbers of birds breeding were relatively stable at ~10 000 pairs for about a decade between 2003 and 2015. Thereafter, they declined sharply over the last 10 years (1G), from ~11 450 pairs in 2014 to ~2 540 pairs in 2023, at an unsustainable annual rate of change of –12.9% (–20.6% to –5.9%), resulting in an overall decline of 88.1% (78.2–94.9%) in the breeding population in that province over the last 30 years (3G). This represents a substantive worsening of both the population trajectory and population status since the 2019 assessment, when the 3G decline was 66.2% and the annual rate of change over the last 1G was –3.5% (Sherley et al. 2020a). If the IUCN Red List criterion A2 were to be applied to the Eastern Cape subpopulation, the species would qualify for the status CR with 93% probability.

Future population projections and Red List status under criterion A4

The IUCN Red List allows for a species to be assessed against the categories based on a “population size reduction...over any 10-year or three-generation period... where the time period must include both the past and

the future” (IUCN 2012; Table 1: criterion A4). Given the concerning loss of ~14 000 breeding pairs in less than a decade, that only ~70% of that number persist today, and that the estimated global decline over the last 3G was very close to the CR threshold (80%) under criterion A2ab, we used the JARA analysis tool to assess the trajectory of the population decline against criterion A4ab. Although the IUCN Red List guidelines allow for projections up to 3G into the future (e.g. under criterion A3; Table 1), the level of uncertainty increases, and the projections become less reliable further into the future. Thus, we used the projection function in JARA to project 10 years of future breeding counts (with uncertainty; Figure 2), with the projections at each of the 26 colonies based on the median annual rate of change at that colony over the final 1G (10 years) of data (Sherley et al. 2020b; Supplementary Figure S2). In this way, we assume that the near future (10 years after 2023) will be like the recent past (10 years prior to and including 2023). We then used a combination of the last 20 years (2G) of observed data and 10 years (1G) of projected data to estimate “moving window reductions” over 3G where the terminal year spanned 2023 to 2033 (the A2 reduction in Figure 1). In other words, each 3G period would span 1993 to 2023, 1994 to 2024, and so on until 2003 to 2033. For each 3G period, we recorded the posterior distribution of all population-change percentages, the posterior median, the best-supported IUCN Red List category based on the posterior distribution, and the probability supporting a listing of CR (Figure 3).

With 2024 as the terminal year of the ‘moving window’, the median decline over 3G was 77.7% (70.6–85.1%), with 27% of the posterior distribution of change percentages exceeding the 80% threshold for a CR listing (i.e. the probability supporting a listing of CR was 27%); thus, an EN listing would remain the best-supported category based on criterion A (Figure 3). However, by 2027 the combination of the observed and projected data indicated that the median decline over 3G would exceed the 80% threshold for a CR listing under criterion A4ab with 56% probability. From 2028 onwards, CR was the best supported category based on criterion A4ab with >95% support in each instance (Figure 3). The projections also suggest that the present decline shows no clear sign of reversing if conditions over the next 10 years reflect conditions in the recent past (Figures 2 and 3).

It is worth noting that approximately 10–20% of mature adults in the African Penguin population appear to skip breeding in any given year (Whittington et al. 1996; Leith et al. 2022); consequently, there may be a large pool of mature nonbreeding adults (Kemper et al. 2007b). As in other seabirds, these nonbreeders may buffer population declines (e.g. Votier et al. 2008). While this means that breeding numbers have the potential to recover rapidly in this population, the results of previous capture-mark-recapture studies on African Penguins indicate that the observed population decline is underpinned by poor annual survival of both mature adults and first-year birds (Sherley et al. 2014, 2017; Leith et al. 2022; see Supplementary Table S1), that most birds that skip reproduction do so for only one year at a time before resuming breeding again (Whittington et al. 1996;

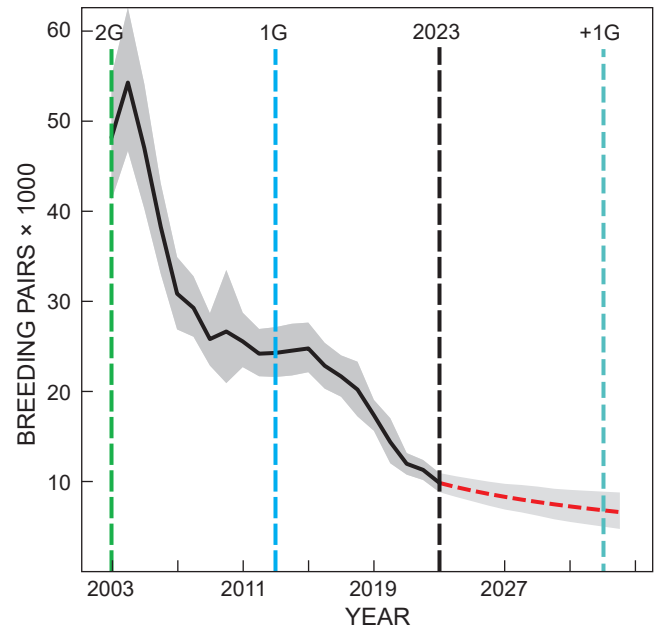


Figure 2: The modelled population trajectory (black line denotes the posterior median) and 95% highest-posterior-density intervals (HPDI; dark grey polygon) for the African Penguin *Spheniscus demersus* breeding population based on observed nest counts made at 26 colonies over the last 2 generations (2G) — that is, between 2003 (vertical dashed green line) and 2023 (vertical dashed black line), and the projected population trajectory (red dashed line) and 95% highest-posterior-density intervals (HPDI; light grey polygon) 10 years, or 1 generation (1G), into the future (+1G). The projections are based on the median annual rate of change at each colony over the final 10-year generation before 2023 (i.e. from the 1G blue dashed line to the 2023 black dashed line)

Leith et al. 2022), and that skipping breeding has not appeared to confer a detectable survival advantage in this species in the past (Wolfaardt et al. 2008; Leith et al. 2022). As a consequence, we propose that the African Penguin has met the IUCN Red List threshold for a global status of CR under criterion A4ab and should now be considered a Critically Endangered species.

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Competing interests statement — RBS and JK are on the Editorial Board of *Ostrich*. RBS is on the Board of Directors of SANCCOB, a registered non-profit company that receives donations and other funding for work on the conservation of seabirds, including the African Penguin.

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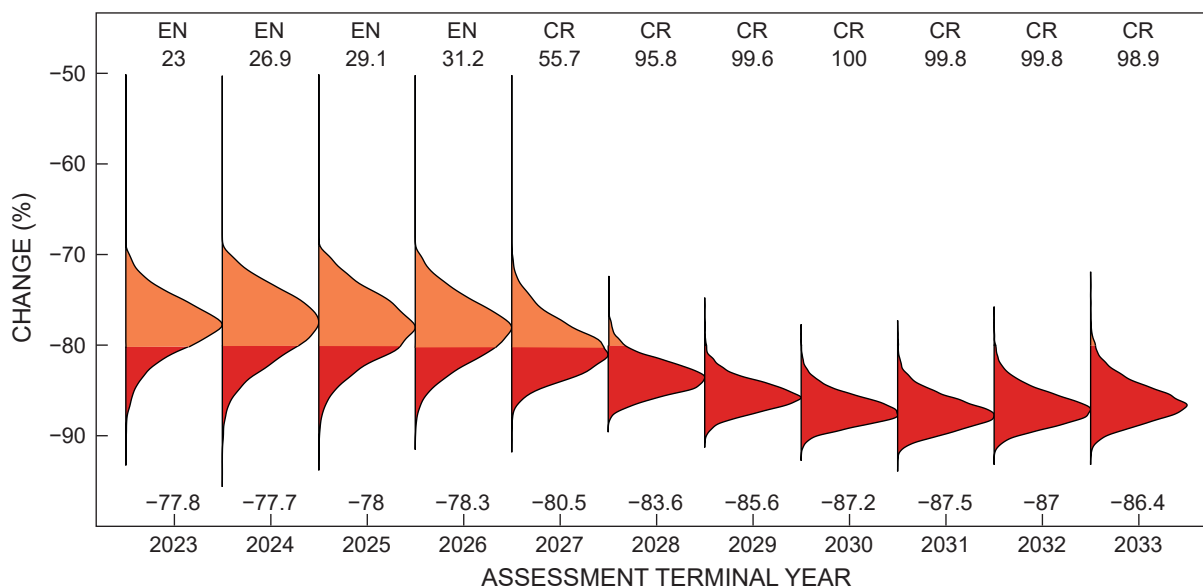


Figure 3: Posterior distribution of population change percentages for assessment of a “moving window reduction” of the global African Penguin *Spheniscus demersus* population against criterion A4ab. Decline percentages are based on a combination of observed and projected data to give 3 generations (3G) where the terminal year spanned 2023 to 2033 (e.g. Figure 2). The left-most distribution is based on the population trajectory between 1993 and 2023 (see the 3G and 2023 lines in Figure 1), and the right-most distribution is based on the trajectory between 2003 and 2033 (see the 2G and +1G lines in Figure 2), with the terminal year of the moving window shifting one year to the right along the x-axis. The median change (%) in the breeding population over each 30-year period is shown above the x-axis (e.g. 83.6% decline for 1998 to 2028). Orange denotes declines that exceed the Endangered (EN) threshold (50% over 3G), and red denotes declines that exceed the Critically Endangered (CR) threshold (80% over 3G). The best-supported global IUCN Red List status at each terminal year (based on criterion A4ab) is shown at the top of the plot, along with the probability that the species will meet the CR threshold (e.g. 55.7% in 2027)

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References

- Brooke RK. 1984. *South African Red Data Book – birds*. South African National Scientific Programmes Report No. 97. Pretoria, South Africa: Council for Scientific and Industrial Research.
- Crawford RJM, Davis SA, Harding RT, Jackson LF, Leshoro TM, Meyer MA et al. 2000. Initial impact of the *Treasure* oil spill on seabirds off western South Africa. *South African Journal of Marine Science* 22: 157–176. <https://doi.org/10.2989/025776100784125645>
- Crawford RJM, David JHM, Shannon LJ, Kemper J, Klages NTW, Roux JP et al. 2001. African Penguins as predators and prey – coping (or not) with change. *South African Journal of Marine Science* 23: 435–447. <https://doi.org/10.2989/025776101784528836>
- Crawford RJM, Underhill LG, Upfold L, Dyer BM. 2007. An altered carrying capacity of the Benguela upwelling ecosystem for African penguins (*Spheniscus demersus*). *ICES Journal of Marine Science* 64: 570–576. <https://doi.org/10.1093/icesjms/fsm009>
- Crawford RJM, Altwegg R, Barham BJ, Barham PJ, Durant JM, Dyer BM et al. 2011. Collapse of South Africa’s penguins in the early 21st century. *African Journal of Marine Science* 33: 139–156. <https://doi.org/10.2989/1814232X.2011.572377>
- Crawford RJM, Sydeman WJ, Tom DB, Thayer JA, Sherley RB, Shannon LJ et al. 2022. Food limitation of seabirds in the Benguela ecosystem and management of their prey base. *Namibian Journal of Environment* 6(A): 1–13.
- Frost PGH, Siegfried WR, Cooper J. 1976. Conservation of the Jackass Penguin (*Spheniscus demersus* [L.]). *Biological Conservation* 9: 79–99. [https://doi.org/10.1016/0006-3207\(76\)90042-2](https://doi.org/10.1016/0006-3207(76)90042-2)
- IUCN (International Union for Conservation of Nature). 2012. *IUCN Red List Categories and Criteria: version 3.1* (2nd edn). Gland and Cambridge: IUCN.
- Kemper J. 2015. African Penguin (Jackass Penguin) *Spheniscus demersus*. In: RE Simmons, CJ Brown, J Kemper (eds), *Birds to watch in Namibia: Red, rare and endemic species*. Windhoek: Ministry of Environment and Tourism, Namibia Nature Foundation.
- Kemper J, Underhill LG, Crawford RJM, Kirkman SP. 2007a. Revision of the conservation status of seabirds and seals breeding in the Benguela ecosystem. In: SP Kirkman (ed.), Final report of the BCLME (Benguela Current Large Marine Ecosystem) project on top predators as biological indicators of ecosystem change in the BCLME. Cape Town: Avian Demography Unit. pp 325–342.
- Kemper J, Roux JP, Bartlett PA, Chesselet YJ, Delpont JA, James JAC et al. 2007b. The African Penguin *Spheniscus demersus*: population estimates, trends, adult survival and age structure from molt and nest counts. In: SP Kirkman (ed.), Final report of the BCLME (Benguela Current Large Marine Ecosystem) project on top predators as biological indicators of ecosystem change in the BCLME. Cape Town: Avian Demography Unit. pp 69–76.

- Leith F, Grigg JL, Barham BJ, Barham PJ, Ludynia K, McGeorge C et al. 2022. Intercolony variation in reproductive skipping in the African penguin. *Ecology and Evolution* 12: e9255. <https://doi.org/10.1002/ece3.9255>
- Rand RW. 1963a. The biology of guano-producing seabirds. 4. Composition of colonies on the Cape Islands. *Investigational Report Division of Fisheries South Africa* 43: 1–32.
- Rand RW. 1963b. The biology of guano-producing seabirds. 5. Composition of colonies on the South West African Islands. *Investigational Report Division of Fisheries South Africa* 46: 1–26.
- Shannon LJ, Crawford RJM. 1999. Management of the African Penguin *Spheniscus demersus* – insights from modelling. *Marine Ornithology* 27: 119–128.
- Shelton PA, Crawford RJM, Cooper J, Brooke RK. 1984. Distribution, population size and conservation of the Jackass Penguin *Spheniscus demersus*. *South African Journal of Marine Science* 2: 217–257. <https://doi.org/10.2989/02577618409504370>
- Sherley RB, Abadi F, Ludynia K, Barham BJ, Clark AE, Altwegg R. 2014. Age-specific survival and movement among major African Penguin *Spheniscus demersus* colonies. *Ibis* 156: 716–728. <https://doi.org/10.1111/ibi.12189>
- Sherley RB, Ludynia K, Dyer BM, Lamont T, Makhado AB, Roux JP et al. 2017. Metapopulation tracking juvenile penguins reveals an ecosystem-wide ecological trap. *Current Biology* 27: 563–568. <https://doi.org/10.1016/j.cub.2016.12.054>
- Sherley RB, Crawford RJM, de Blocq AD, Dyer BM, Geldenhuys D, Hagen C et al. 2020a. The conservation status and population decline of the African Penguin deconstructed in space and time. *Ecology and Evolution* 10: 8506–8516. <https://doi.org/10.1002/ece3.6554>
- Sherley RB, Winker H, Rigby CL, Kyne P, Pollom R, Pacoureaux N et al. 2020b. Estimating IUCN Red List population reduction: JARA – a decision-support tool applied to pelagic sharks. *Conservation Letters* 13: e12688. <https://doi.org/10.1111/conl.12688>
- Votier SC, Birkhead TR, Oro D, Trinder M, Grantham MJ, Clark JA et al. 2008. Recruitment and survival of immature seabirds in relation to oil spills and climate variability. *Journal of Animal Ecology* 77: 974–983. <https://doi.org/10.1111/j.1365-2656.2008.01421.x>
- Whittington PA, Hofmeyr JH, Cooper J. 1996. Establishment, growth and conservation of a mainland colony of Jackass Penguins *Spheniscus demersus* at Stony Point, Betty's Bay, South Africa. *Ostrich* 67: 144–150. <https://doi.org/10.1080/00306525.1996.9639700>
- Winker H, Pacoureaux N, Sherley RB. 2020. JARA: 'Just Another Red-List Assessment'. *bioRxiv*: 672899. <https://doi.org/10.1101/672899>
- Wolfaardt A, Underhill L, Altwegg R, Visagie J. 2008. Restoration of oiled African penguins *Spheniscus demersus* a decade after the Apollo Sea spill. *African Journal of Marine Science* 30: 421–436. <https://doi.org/10.2989/AJMS.2008.30.2.14.564>